

A Coral-Eating Barnacle

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ABSTRACT: Many rock barnacles form close associations with other organisms, yet none are known to have become wholly parasitic. In a study of balanids inhabiting corals, we encountered a species—*Pyrgoma monticulariae* Gray, 1831—that depends on the coral for both habitat and food. In achieving this relationship it has gained control over certain metabolic activities of the coral, including calcification, proliferation of coenenchyme, and nematocyst discharge. While balanids became associated with corals 25 million years ago, evidence suggests that this wholly parasitic relationship has developed within the last 10 million years.

CERTAIN ROCK BARNACLES live in association with corals (Hiro, 1938; Nilsson-Cantell, 1938). Whereas some species gradually become engulfed and eventually overgrown, others are specifically modified for this habitat by having adapted morphologically and physiologically to the growth pattern of the coral.

A critical problem in the association is maintenance by the barnacle of free communication with the surrounding water in order to carry on normal physiological processes—gathering food, mating, releasing larvae, and voiding wastes. In generalized or primitive coral barnacles, an opening to the exterior is maintained by cirri, which mechanically clean away obstructions. But, as in all rock barnacles, six pairs of bristle-bearing cirri are extended to form a net employed in setose filter feeding. Such forms can be considered semiparasitic in that they depend on the coral for habitat but not for food.

In a revisionary study of the coral-inhabiting balanomorph barnacles *Pyrgoma* and *Creusia*, we encountered specimens of the little known Indo-Pacific species, *Pyrgoma monticulariae* Gray (1831). The shell of this species has been described in detail (Hiro, 1935, 1938). Its distinguishing characteristics are an extraordinarily irregular outline and, in proportion to the size of the shell, an extremely small aperture (Fig. 1A). In the specimens available from Mauritius

in the Indian Ocean, a layer of tissue was found growing over the entire exterior of the shell, apparently sealing the barnacle off from the external milieu. Squashed preparations of this tissue revealed numerous nematocysts, indicating that the tissue is an extension of the coral coenenchyme.

Dissection revealed *P. monticulariae* has but one pair of biramous cirri, and these are unusually formed (cf. Figs. 2C and F). The slender rami are clearly no longer adapted for filter feeding, but rather appear to be antenniform sensory structures. The remaining five pairs of cirri are recognizable as stubs or vestigial limbs supporting few or no setae. The antenniform pair of cirri is interpreted as being the fourth, not only because of its sequential occurrence, but because in balanids the first three pairs are ordinarily closely associated with the mouth, and hence would not be likely candidates for sensory structures. Of the three posterior pairs of cirri, two are vestigial, but they are posterior to the origin of the intromittant organ, which has migrated to a more anterior position. So organized, the mouth parts, the single pair of cirri, and the intromittant organ are concentrated in the vicinity of the minute aperture (cf. Figs. 1B and D).

The mouth field, as compared with other species in this group, is also unusual; it is produced into a remarkably long, slender cone. The mandibles have relatively simple, straight, sawlike cutting edges instead of a few strong teeth, and produced molariform lower angles (cf. Figs. 2A and D). The first maxillae are

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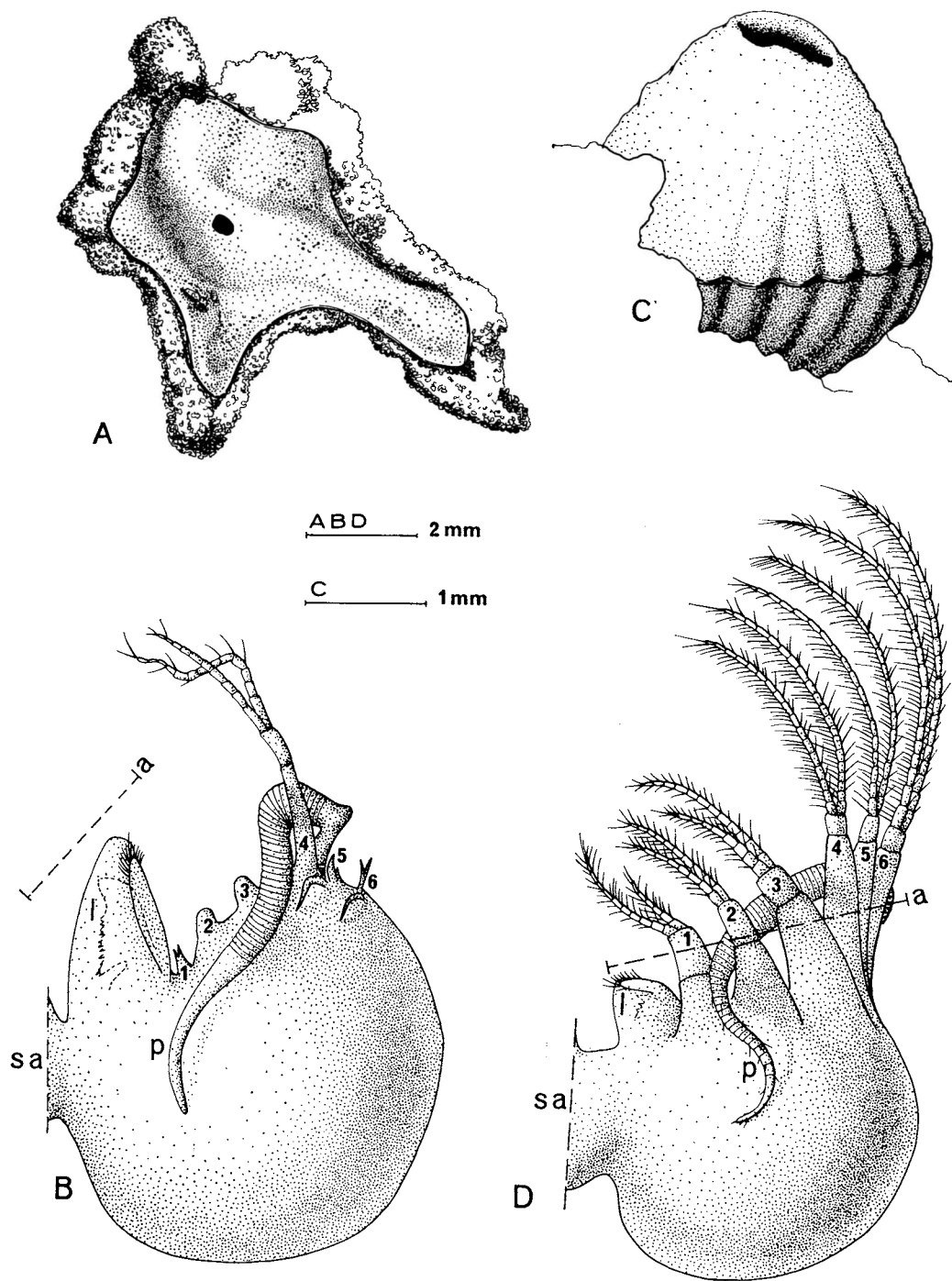


FIG. 1A-D

A, *Pyrgoma monticulariae* (Gray), 1831. External surface of peltate shell viewed from above, showing irregular outline and extremely small central aperture.

B, *Pyrgoma monticulariae*. Body viewed from right side showing labrum forming oral cone, distended stomach (thorax), vestigial cirri 1, 2, 3, 5, and 6, and antenniform cirrus 4.

C, *Pyrgoma anglicum* (Sowerby), 1823. External view of shell and portion of basis from left side, illustrating high conic form and normal aperture.

D, *Pyrgoma anglicum*. Body viewed from right side showing normal development of trophic structures, cirri and thorax. *a*, Relative size of aperture; *l*, labrum enclosing mouth parts; *p*, penis; *sa*, site of attachment to scutal valves.

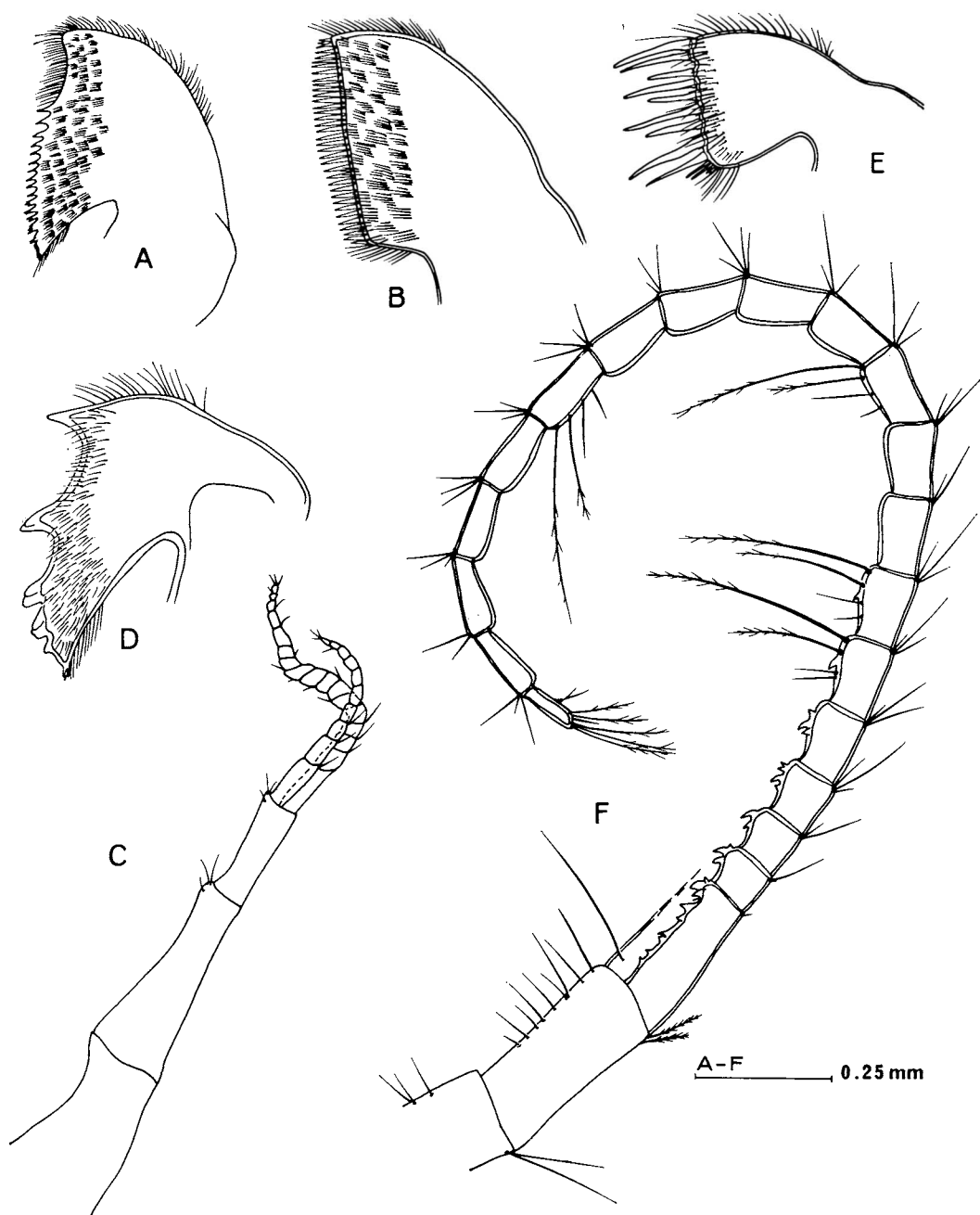


FIG. 2A-F

- A, *Pyrgoma monticulariae* (Gray), 1831. Mandible modified as sawlike blade.
 B, *Pyrgoma monticulariae*. Maxilla I modified in same manner as mandible.
 C, *Pyrgoma monticulariae*. Cirrus 4 much reduced and modified as antenniform appendage.
 D, *Pyrgoma anglicum* (Sowerby), 1823. Normal mandible with incisive upper teeth and molariform lower angle.
 E, *Pyrgoma anglicum*. Normal maxilla I with spines arranged in functional groups.
 F, *Pyrgoma anglicum*. Normal filter feeding cirrus 4 with hooks along anterior border.

comparable in form, having simple, sawlike edges, rather than a variety of spines arranged in functional groups (cf. Figs. 2B and E). The labrum is abnormally elongate, and forms the anterior and lateral borders of the oral cone (Fig. 1B). The lateral margins of the cone are flanked by long, narrow palps, and the cone is closed to the rear by a completely fused pair of second maxillae. The space within the distended thorax contains a large stomach, the content of which consists of macerated tissue and an abundance of undischarged nematocysts.

The presence in the stomach of nematocysts and macerated tissue, rather than crustacean, molluscan, and protozoan fragments and detritus, when considered along with the morphological modifications described above, indicates that this species is feeding on coral tissue, and therefore it can be classified as wholly parasitic. This is in contrast to such forms as *Hermodice carunculata* (Pallas), a coral-eating polychaetous worm, which moves about feeding on the tips of coral colonies, and therefore is considered a predator (Marsden, 1962).

Although no direct observations have been made, the feeding process can be inferred. *Pyrgoma monticulariae* has apparently gained metabolic control of the coral, preventing skeletal material formed by the coral coenenchyme from over-growing it, while simultaneously inducing rapid proliferation of coenenchyme in the apertural area. The coenenchyme grows not only over but into the aperture, and the sawlike mouth parts of the barnacle are especially modified to be applied from below and rasp it away.

Metabolic activities such as exchange of O_2 and CO_2 , and excretion of soluble nitrogenous wastes evidently take place through simple diffusion across investing host structures. The problems of voiding solid wastes, releasing larvae, and mating would require clearing a passage to the exterior. We have no evidence that this actually happens, but the relatively large intromittant organ suggests that cross fertilization must occur at least occasionally, and the sensory nature of the surviving pair of cirri suggests that this structure may be involved in mating (Fig. 1B). The form and orientation of the trophic structures indicate that they could be applied to clearing this passage when necessary.

It is not uncommon for a free-living organism that becomes associated with another to establish eventually a wholly parasitic relationship. Only two cases are known in true barnacles—*Anelasma squalicola* on certain dogfish (Johnstone and Frost, 1927), and *Rhizolepas annelidicola* on an errant polychaetous annelid (Day, 1939). In both of these lepadomorphs, parasitism has been established by extending nutrient-absorbing processes into the host tissues, and feeding structures no longer necessary have become vestigial or lost. *Pyrgoma monticulariae* differs from these in that its nutritional requirements are satisfied through modification of the basic feeding mechanism rather than by the development of separate absorptive processes.

The evolution of *P. monticulariae* is remarkably clear because virtually the entire range of intergrading species, from free living to wholly parasitic, is living today. The first important step made in establishing this association with corals was control over skeletal formation, an ability well known in other crustaceans (Potts, 1915). Barnacles in this sequence had already developed the ability to keep the aperture clear by activity of the appendages (Fig. 2F). The material cleared has to be removed from these appendages, and normally this is accomplished during the feeding process (Darwin, 1854). Thus, this material is likely to be ingested, and additional nutriment acquired in this way would augment the diet. An as yet unidentified species presently under study is intermediate in structure between normal and parasitic forms, apparently obtaining part of its food by setose feeding and part by rasping tissues of the host coral with its mouth parts. *P. monticulariae* acquires from the coral sufficient food for its total sustenance, apparently by irritating or metabolically inducing coenenchyme to proliferate in areas being cleaned.

The retention of a number of vestigial appendages in *P. monticulariae* suggests that its adaptation is relatively recent, or that the juvenile stages still feed by setose methods while becoming established. The group from which *Pyrgoma* descended appears in the Miocene, but *Pyrgoma* itself, not until the Pliocene (Withers, 1929; Baluk and Radwanski, 1967); therefore, the relationship is probably no more than 10 million years old.

P. monticulariae poses many interesting problems for biologists, but these must be approached through the study of living specimens. To begin with, it would be extremely interesting to know if early stages of this species are initially setose feeders, and at what subsequent stage they shift to a parasitic mode of feeding. It would also be of considerable interest to investigate control of calcification and host tissue proliferation, reproductive behavior, and other aspects of general biology alluded to here.

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LITERATURE CITED

- BALUK, W., and A. RADWANSKI. 1967. Miocene cirripeds domiciled in corals. *Acta Palaeontologica Polonica*, vol. 12, pp. 457-521.
- DARWIN, C. 1854. A monograph on the subclass Cirripedia; the Balanidae, the Verrucidae, etc. London, Ray Society. viii + 684 pp., 30 pls.
- DAY, J. H. 1939. A new cirripede parasite—*Rhizolepas annelidicola*, nov. gen. et sp. *Proceedings of the Linnean Society, London*, vol. 151, pp. 64-79.
- GRAY, J. E. 1831. Description of two new species of serpula, and an undescribed coral barnacle, discovered by Samuel Pearce Pratt, Esq. *Zoological miscellany*. London, Treuttel, Wurtz and Co. Pp. 1-86.
- HIRO, F. 1935. A study of cirripeds associated with corals occurring in Tanabe Bay. *Records of Oceanographic Works in Japan*, vol. 7, no. 1, pp. 1-28.
- . 1938. Studies on animals inhabiting reef corals. II. Cirripeds of the genera *Creusia* and *Pyrgoma*. *Palao Tropical Biological Station Studies*, vol. 3, pp. 391-416.
- JOHNSTONE, J., and W. E. FROST. 1927. *Ane-lasma squalicola* (Lovén): its general morphology. *Proceedings and Transactions of the Liverpool Biological Society*, vol. 41, pp. 29-91.
- MARSDEN, J. R. 1962. A coral-eating polychaete. *Nature*, vol. 193, p. 598.
- NILSSON-CANTELL, C. A. 1938. Cirripedes from the Indian Ocean in the collection of the Indian Museum, Calcutta. *Memoirs of the Indian Museum*, vol. 13, pp. 1-81.
- POTTS, F. A. 1915. *Hapalocarcinus*, the gall forming crab with some notes on the related genus *Cryptochirus*. *Papers from the Tortugas Laboratory (Department of Marine Biology) of the Carnegie Institution*, vol. 8, pp. 33-69.
- WITHERS, T. H. 1929. The phylogeny of the cirripedes *Creusia* and *Pyrgoma*. *Annals and Magazine of Natural History*, ser. 10, vol. 4, pp. 559-566.